Flower buds and the directions of floral evolution

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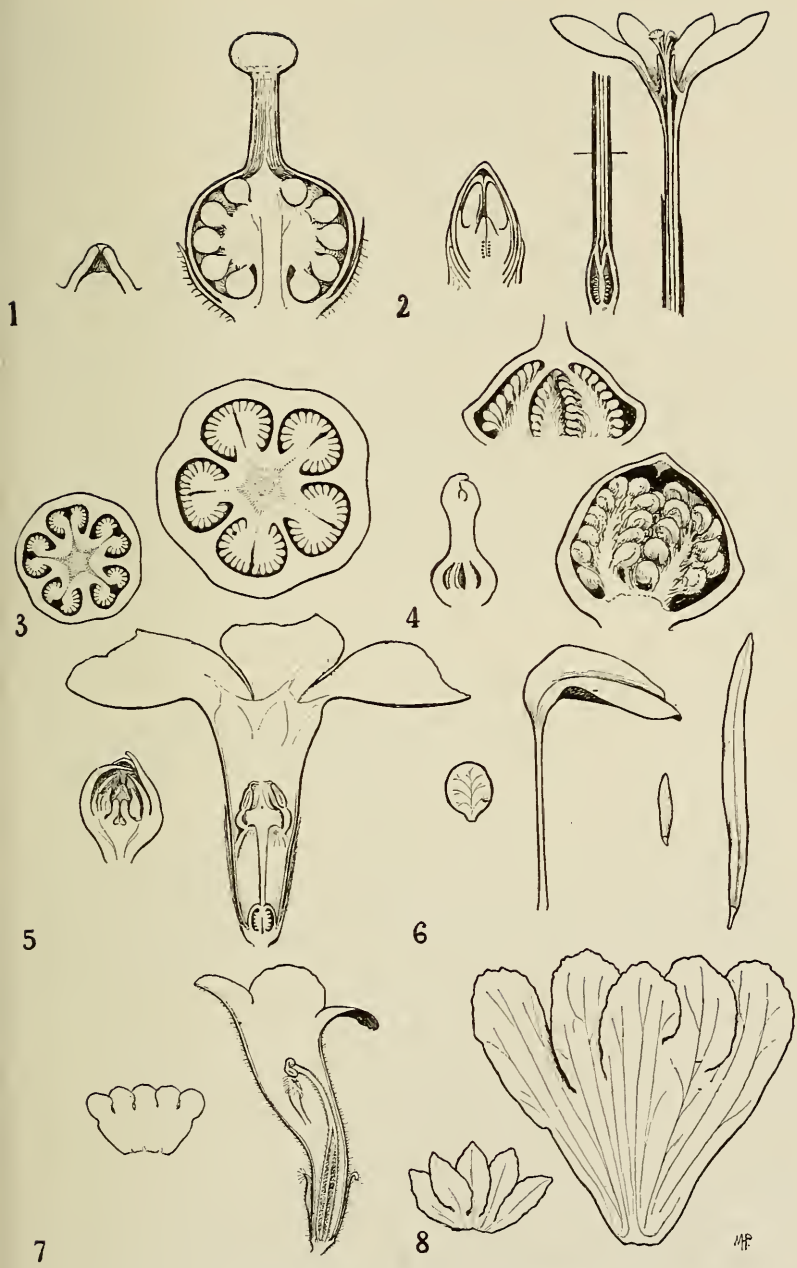
The comparison of the structure of flower buds with that of adult flowers is an interesting study. Such characters as an inferior ovary, an irregular or sympetalous corolla, or epipetalous stamens are evidently modern improvements. All are relatively less developed in the bud than in the adult flower.

The drawings by Miss Maud Purdy illustrate the development of various characters:

1. *Primulaceae—Primula obconica*
   Style and stigma absent in bud, very distinct in adult flower.
2. *Iridaceae—Crocus vernus*
   Ovary, from superior to inferior.
3. *Ericaceae—Rhododendron indicum*
   Placentation, suggestion of change from parietal to axile.
4. *Portulacaceae—Portulaca grandiflora*
   Placentation, suggestion of change from parietal to central. Three placentae early detach from the walls. Finally the united upper part withers, making apparently three central or basal placentae.
5. *Apocynaceae—Vinca minor*
   Stamens, from hypogynous to epipetalous.
6. *Cruciferae—Cheiranthus kewensis*
   Hamamelidaceae—Loropetalum chinense
   In the buds the petals have the ordinary ovate form; the claw of the petal of *Cheiranthus* and the linear petal of *Loropetalum* develop later.
7. *Gesneriaceae—Chirita lavandulacea*
   Corolla from regular to irregular; in the bud the corolla is nearly regular.
8. *Caprifoliaceae—Lonicera fragrantissima*
   In the bud the united part of the corolla is a fourth or less of the whole, in flower more than half. Similar change is the rule among *Sympetalae.*

That floral development in a general way suggests lines of evolution cannot be doubted. Among recent summaries of evolutionary directions of flowering plants are those by Diels in



Flower Buds compared with Flowers

1920, by Sprague in 1923, by Hutchinson in 1926 and by Zimmermann in 1930. A very brief outline follows:

Ovules and Seeds

1. Ovules many→few
2. Embryo straight→curved
3. Endosperm present→absent
4. Seedcoats 2→1

The number of ovules developing into seeds decreases in the higher flowering plants. We see a similar evolution in the animal world. For example, in fishes thousands or even millions of eggs are laid. In mammals, only a few young are born, but these are given better care. Many plants with a curved embryo grow in dry climates where quick germination is important. In the case of the *Centrospermae* a curved embryo is nearly universal; an exception is *Dianthus* and related genera, with embryo nearly straight. In the Engler system these genera come at the end of *Centrospermae*. Should they be the beginning and thus connect with *Frankenia?*

Carpels

1. Carpels many→few
2. Separate→partly united→wholly united
3. Ovary superior→half inferior→wholly inferior
4. Placentation parietal→central
   →axile

United carpels, an inferior ovary, and axile placentation are all tendencies in the same direction, namely for better protection of the seed. Another specialized character is partly sterile carpels. The absence or near absence of style and stigma must be considered as primitive. Basal placentation may perhaps be primitive in some cases and derived in others.

Stamens

1. Stamens numerous→2 whorls→1 whorl
2. Free→more or less united
3. From receptacle→from petals
4. Filaments broad→filiform

Stamens few is a character of the advanced flowers. With improved methods of pollination, less pollen is needed. Lin-

naeus' classification depended on the number of stamens. He began with one stamen; now the sequence must be reversed. Plants with many stamens have in numerous cases also other primitive characters. Stamens in part sterile, or pollen grains more or less united are specialized characters.

Perianth

1. Sepals and petals nearly alike→clearly differentiated
2. Perianth parts many→few
3. Sepals and petals free→more or less united
4. Arrangement spiral→hemicyclic→cyclic
   This fourth series is questioned by Sprague.
5. Regular (actinomorphic)—irregular (zygomorphic)

Comparatively few changes occur in the calyx. Separate sepals are the exception, they occur chiefly in the *Magnolia* and *Parietales* groups. In the corolla of insect pollinated flowers the changes are in the direction of improved adaptation to insect visitors. The evolution of flowers must have proceeded parallel to that of insects. Petals with claws, etc. as in many *Cruciferae*, or flowers with special structures, such as a corona, must be considered as specialized forms.

Receptacle

1. Convex→flat→concave
2. Disk absent→present

Inflorescence

1. Flowers solitary→inflorescence loose→inflorescence condensed
2. Flowers alike→more than one kind of flower
3. Flowers perfect→polygamous→monoecious→dioecious

Vegetative Parts

1. Leaves simple→compound (?)
2. Lacunae at nodes below leaf bases, 3→1 (Sinnott)
3. Trees or shrubs→herbaceous perennials→annuals
4. Vessels scalariform→pitted

Finally, in addition to the evidence from ontogeny, other and entirely independent lines of investigation may throw light on floral evolution. First of these comes paleobotany. It is of special interest that the dicotyledonous genera from the Cre-

taceous are nearly all woody plants with scalariform vessels. Further, evidence from plant serums may be looked upon as of significance, without considering it as all-conclusive. Also the fact that leaf-eating insects may choose related species for their attacks is significant; it looks as if insects discovered plant families before the botanists. Similarly, plant pathology shows us that fungous parasites often select host plants of related forms.

"Characters must be weighed rather than counted," said Bernard de Jussieu, commenting on the numerical system of Linnaeus. In the old systems, beginning with Tournefort, too much weight may have been attached to the character of sympetaly. In the Bessey system the character of superior or inferior ovary may have been given too much weight. Again in the Hutchinson system the character of woody versus herbaceous plants may have been over-emphasized. In the future the natural classification of the higher plants will gradually develop and it will include all characters. "The jewels in the crown of phylogeny," says Zimmermann, "will only then become significant, when all are together, their beauty many times enhanced by their mutual reflections."

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